AN APPARENT CASE OF INTROGRESSION BETWEEN PINYON PINES OF THE NEW YORK MOUNTAINS, EASTERN MOJAVE DESERT

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ABSTRACT

The pinyon pines in the New York Mountains of the Mojave Desert are polymorphic along an altitudinal gradient. The possibility that this gradient is the result of hybridization between *Pinus monophylla* and *P. edulis* is the subject of this study. Counts of needle number per fascicle, resin canal number per needle, and cone width were made over the entire altitudinal range of distribution of the pine community. We conclude that there are two species present and that an extensive altitudinal zone of introgression exists at intermediate elevations.

The characterization of the pinyon pines in the New York Mountains, San Bernardino County, California, has been addressed by several authors (Lanner 1974, Vasek and Thorne 1977, Trombulak and Cody 1980, Thorne et al. 1981). The slopes of the New York Mountains are described as containing the westernmost sympatric distribution of *Pinus edulis* and *P. monophylla* (Griffin and Critchfield 1972). Lanner (1974), however, concluded that *P. monophylla* is the only species present and that the two-needle form represents a mutant to the ancestral two-needle condition. His argument was based on the resemblance of other morphological characters to those of *P. monophylla*. Trombulak and Cody (1980) found that the proportion of two-needle fascicles on individual trees showed a nearly disjunct distribution with practically no trees displaying intermediate proportions, and concluded that both *P. monophylla* and *P. edulis* were present with the latter species limited to higher elevations. Their transects were near Prospect Canyon on the north side of New York Peak.

Reported here are the results of a new study carried out in a south-facing drainage on the same mountain. We describe an altitudinal zone of intergradation between the one- and two-needle forms and speculate on its significance.
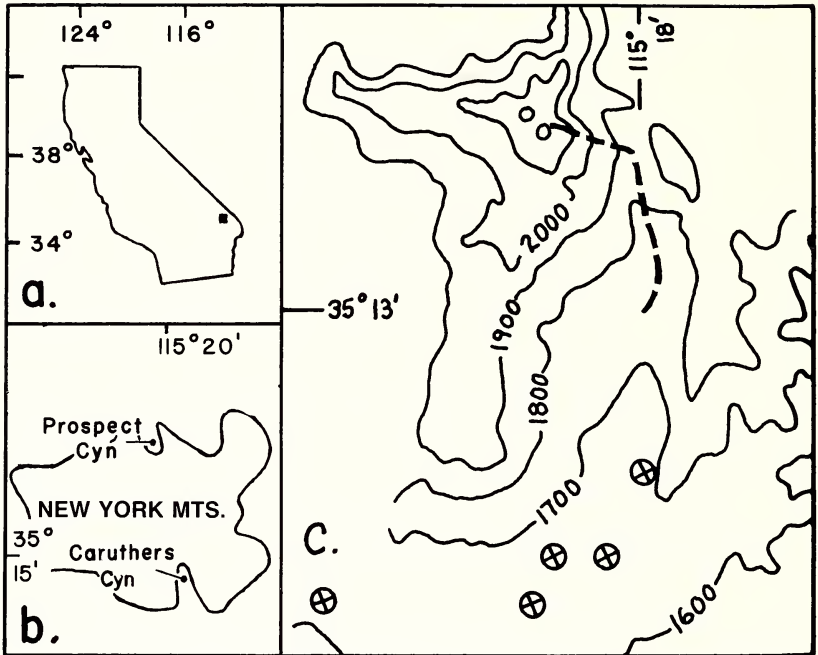
Fig. 1. Location of the transect. a. Map of California. Dark square shows location of New York Mountains. b. New York Mountain range showing both Prospect and Caruthers Canyons. c. Topographic map with 100 m contour intervals showing transect location (dashed line) in Caruthers Canyon. The 5 isolated stations (⊗) are on outcrops at the lower limit of pinyon distribution.

STUDY SITE AND METHODS

Data were collected during the month of May in the years 1981–1985. A transect was placed in the Caruthers Canyon drainage (Fig. 1). The transect followed the jeep road north from the lower limit of pinyons at an elevation of 1620 m to the Giant Ledge Mine, then up an east-facing slope to the peak. The sampling stations along the transect tended to occupy the more mesic situations in the drainage. Elevations and positions were determined using a Thommen temperature compensated altimeter and by triangulation using a Brunton Pocket Transit and USGS topographic maps (Ivanpah, CA, and Midhills, CA, quadrangles).

At 5–60 m increments in elevation, 8–25 trees were sampled. The terminal 15–20 cm segment of a twig was taken at about chest height from the side of the tree most exposed to illumination. From the cut end of the twig the first 20 fascicles were classified as bearing one or two needles. Three-needle fascicles were reported as two-

needle ones. The mean number of two-needle fascicles was computed for each collecting station.

Resin canal numbers were determined from an additional 11–15 twigs (one twig per tree), obtained at each station in a manner similar to that described above. Trees were selected for sampling without regard to which had been sampled previously for fascicle ratio. Five needles were selected at random from near the cut end of each twig. Counts of resin canals in razor-sectioned needles were made under a $10\times$ hand lens. When two-needle fascicles were sampled only one of the two needles was counted.

Sampling was repeated at all but the highest two stations, where measurements of fascicle ratio and resin canal numbers were taken from one twig from each of ten trees at each station. Each twig yielded 20 fascicle counts and five resin canal counts.

Thirty intact seed cones were collected haphazardly from the ground at each station. Vernier calipers were used to obtain the greatest diameter of each cone, to the nearest 0.1 mm.

RESULTS

The frequency of one- and two-needle fascicles on individual trees is shown in Fig. 2B. Of the 388 trees sampled, 122 (31%) showed a range between 20–80 percent two-needle fascicles. A strong altitudinal shift occurred in the proportion of two-needle fascicles.

The proportion of two-needle fascicles (Y) plotted against elevation (X) is illustrated in Fig. 3. The proportion of two-needle fascicles rises sharply between 1700–1900 m and then changes more slowly to the peak. The data are best described by the sigmoid equation

$$Y = \frac{20}{1 + 1.21 \times 10^{49}X^{-14.93}} \quad r^2 = 0.89, \quad p \ll 0.01. \quad \text{(eq. 1)}$$

The elevation at which 50 percent of the sampled fascicles contain two needles ($X_{0.5}$, the turnover elevation) is computed from the regression equation to be 1940 m.

The average number of resin canals per needle (Y) is plotted against elevation (X) (Fig. 3). The average number of resin canals per needle declines sharply between 1620–1860 m. From that elevation to the peak, the number of resin canals changes only slightly (Fig. 3). The data are described best by the sigmoid equation

$$Y = \frac{9}{1 + 7.50 \times 10^{-25}X^{7.38}} \quad r^2 = 0.87, \quad p \ll 0.01. \quad \text{(eq. 2)}$$

The mean number of resin canals for all needles sampled below 1900 m equals 5.5 ± 0.9, n = 950 ($\bar{X} \pm 95\%$ confidence interval). This
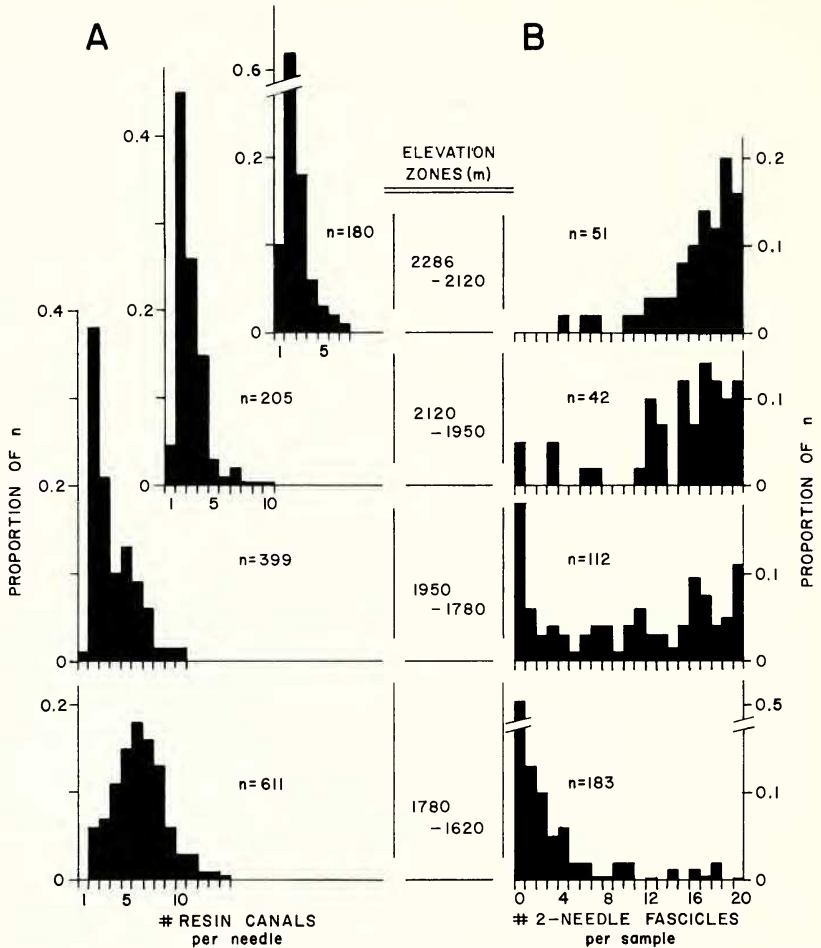
Fig. 2. A. Frequency distribution of the proportion of the sample of needles (n) against resin canal number per needle in four elevation zones. B. The proportion of individual tree samples (n) is plotted against the number of two-needle fascicles per 20 needle sample in four elevation zones.

value does not differ significantly from that reported for *P. monophylla* (4.9 ± 1.1) by Lanner (1974). For the trees above 1900 m the number of resin canals equals 2.7 ± 0.2, n = 445. Lanner's value for *P. edulis* (2.0 ± 0.1) is smaller than that we obtained. The mean resin canal number above 1900 m is significantly lower (t = 4.12; p < 0.001) than it is at lower elevations.

There is a highly significant correlation (t = 8.23, p ≪ 0.01) between the mean number of two-needle fascicles and the mean number of resin canals per needle (Fig. 4). The values near the x-axis are
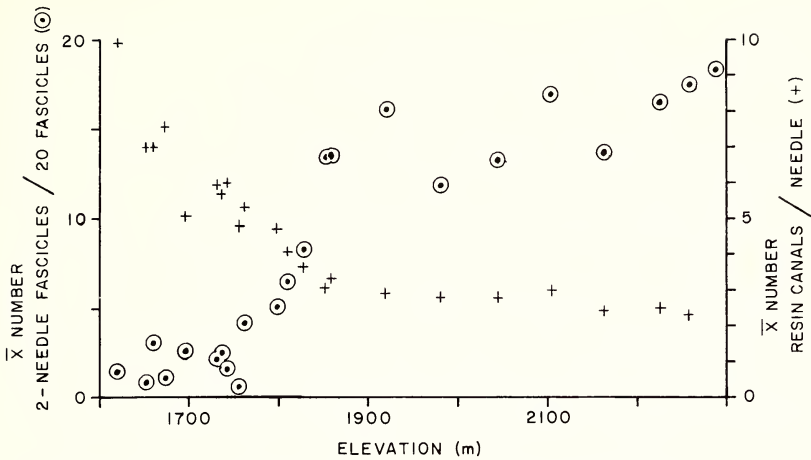
FIG. 3. Change in the mean number of two-needle fascicles per 20 fascicle sample over elevation (circles) and the change in mean number of resin canals per needle over elevation (crosses). Needle number is plotted to the left and resin canal number is at the right.

from sites at the highest elevations and are typical of *P. edulis*. The values near the y-axis are from low elevation sites and resemble *P. monophylla*. The intermediate points are from stations at intermediate elevations.

Seed cone diameter varies independently of elevation. The mean maximum cone diameter for the entire sample equals 54.8 ± 2.5, n = 660. This value is not significantly different from Lanner's (1974) value for widely dispersed hybrid populations in the western U.S. (53.2 ± 5.9, range 30–87 mm). Lanner also reports cone diameters for *P. edulis* and *P. monophylla* as 42.5 ± 4.6, range 20–68 mm and 64.6 ± 4.8, range 39–80 mm, respectively.

DISCUSSION

Lanner (1974) concluded that the ratio of one-needled to two-needled fascicles is heritable. Experimental *P. monophylla* × *P. edulis* hybrids exhibited a 0.5 ratio. In comparing mesic and xeric sites, he also concluded that for *P. monophylla* the ratio is stable and insensitive to site differences.

The transition of trees with one-needle fascicles and several resin canals at lower elevations and on arid slopes toward two-needle, two-resin-canal plants in higher, presumably moister locations is compatible with expectations about *P. monophylla* and *P. edulis*. Trombulak and Cody (1980) present a scenario of progressive replacement of *P. edulis* by *P. monophylla* upward on the slopes in-
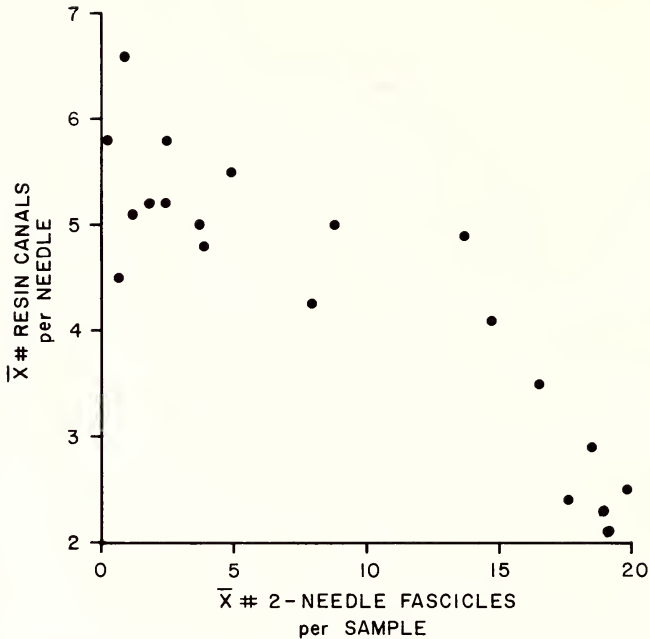
Fig. 4. Relationship between the mean number of two-needle fascicles per 20 fascicle sample and the mean number of resin canals per needle per 50 needle sample. Each point represents one sample station containing 10 trees.

duced by generally more arid conditions since pluvial times. The $X_{0.5}$ needle ratio values they obtained (1680 m and 1834 m) are lower on north-facing slopes than is the value we obtained (1940 m, computed from equation 1) on the south side of the range (Fig. 3). We would add that frost hardiness, especially in seedlings, may be greater in *P. edulis* (R. M. Beeks, pers. comm.), thus making it a superior competitor only at greater elevation and on north-facing slopes. Together these results are consistent with the Trombulak and Cody interpretation of an interaction between the two taxa that is mediated by moisture and temperature (see also Wells 1979, 1983).

The decline in resin canal number that occurs over the same altitudinal range (Figs. 2A, 3) supports the evidence that a zone of intergradation exists between the two taxa. This trait, however, is highly sensitive to site differences. Lanner (1974) showed a 40 percent increase in the number of resin canals in *P. monophylla* when the samples from arid sites ($\bar{X} = 5.06$ canals) were compared to mesic ones ($\bar{X} = 3.62$ canals) in the Raft River Mountains, Utah. The impact of this moisture response in our study is minimized by our deliberate choice of mesic sites to sample. This shifting relationship of needle number to resin canal number (Fig. 4) is a pattern

found elsewhere in hybrid swarms of *P. monophylla* × *P. edulis* (Lanner 1974). Alternatively, but less parsimoniously, the pattern of intergradation might be produced by primary differentiation of altitudinal races or species.

Finally, seed cone size variation is chaotic. The population mean, however, is the same as that obtained for hybrid populations elsewhere in the southwestern U.S. (Lanner 1974). Because this trait overlaps broadly in the two species, it is of little value here in attempting to characterize hybrids.

Endler (1982) defined the width of contact zones between hybridizing species as the region having hybrid index values between 0.2 and 0.8. A substantial number (31%) of the individuals in our sample have those intermediate proportions of two-needle fascicles at middle elevations (Fig. 2B). The distribution shown in Fig. 2B differs significantly ($\chi^2 = 202$; $p < 0.001$) from that obtained by Trombulak and Cody (1980, p. 64). They found practically no trees having intermediate proportions of two-needle fascicles in Prospect Canyon on the north side of New York Peak. They interpret their result as distinguishing clearly between *P. monophylla* and *P. edulis* in the New York Mountains. The distinction fails in Caruthers Canyon, on the south side. In fact, the pattern demonstrated (Fig. 3) shows a zone of intergradation and suggests introgression between about 1700 and 1900 m elevation.

In conclusion, the trees near the peak appear to be a remnant stand of *P. edulis* whose distinctiveness is reduced by hybridization with the regionally abundant *P. monophylla*. The fact that populations in Caruthers and Prospect Canyons show different patterns is particularly interesting. Any explanation for the difference awaits further study.

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ANNOUNCEMENT

Symposium to Honor G. Ledyard Stebbins

An International Symposium will be held in Davis, California, on 12–14 September 1986, to honor Professor G. Ledyard Stebbins in the year of his 80th birthday. Invited talks by leading plant biologists will include topics in population and ecological genetics, organelle and nuclear molecular genetics, morphogenesis and plant development, and evolution and systematics. For further information please contact: Dr. L. D. Gottlieb, Department of Genetics, or Dr. S. K. Jain, Department of Agronomy and Range Science, University of California, Davis, CA 95616.